A REVIEW OF THE AUSTRALIAN CRETACEOUS LONGIPINNATE ICHTHYOSAUR *PLATYPTERYGIUS*, (ICHTHYOSAURIA, ICHTHYOPTERYGIA)

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Platypterygius has hitherto been recognised by its pectoral fins, but it also possesses other unique features. Radiate-textured growth extends the maxilla to the nasal, dividing the area of the primitive elongate naris into a small, nearly oval, naris and an anteronarial *maxillary foramen*. The neural canal groove on the basioccipital tapered, to end less than half-way across the dorsal surface, so the neural cord turned upward at the occipital joint posterior to the exoccipitals. These latter bones were held together by a flexible sheet of connective tissue posteriorly, and the foramen magnum was mainly within the supraoccipital. Neural arches 1 to 32 were strongly reclined and neural spines 11 to 20(+?) had apical notches which presumably betray the existence of a large dorsal fin above the centre of gravity. Beginning about vertebrae 28-32 the zygapophysial facets were gradationally re-aligned from approximately 30° to vertical.

The new species *Platypterygius longmani* is erected on the basis of the best available material. This new taxon accommodates the species apparently represented by the indeterminate fragments *Ichthyosaurus australis* McCoy (1867), *I. marathonensis* Etheridge (1888) and many better specimens, all from the Albian of Queensland.

All known Australian ichthyosaurs were preserved in oxygenated environments and have floated and lost extremities during decomposition after death. Euxinic environments contain many individuals that never floated, consequently the extremities are much more likely to be preserved.

☐ *Reptilia, Ichthyosauria, Longipinnate, Platypterygius longmani, Cretaceous, Queensland.*

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De Vis, who we are honouring in this Symposium, came too late on the scene to describe the first Australian ichthyosaurs. These were collected near O'Connell Creek, a tributary of the braided Flinders River in North Queensland, by James Sutherland in 1865 and 1866, and were despatched promptly from Marathon Station to Professor M'Coy (or McCoy as he later spelt his name) for the collections at the Museum of Victoria (M'Coy, 1867, 1869).

The general area of these finds was in the upper Albian, part of a re-flooded Euroka Strait (Smart & Senior, 1980). This was the intake for ocean water into the Eromanga Basin Sea, across a broad sill between the Mt Isa and Georgetown Precambrian blocks. While the upper waters teemed with fish, cephalopods, and their predators, the sea floor had a restricted, almost monospecific, *Inoceramus* fauna. Perhaps this monotonous benthic fauna reflected a slightly hypersaline counter-current such as that which flows out of the Mediterranean just above the sill between Gibraltar and Africa. Further into the basin gypsiferous silts and shales interdigitate with fish-debris limestones or 'cannonball' concretions, as at 'Canary' Station near Boulia, NW Queensland. Together all these beds constitute the Toolebuc Formation. Charles and Andrew Robinson of 'Canary' have located five incomplete but identifiable ichthyosaurs to date, and a sixth example has just been collected there, with the skull and cervical vertebrae of a large embryo in the same nodule as part of the ribs of the adult. To the north the Allaru Mudstone overlies the Toolebuc Formation, and going east, it extends stratigraphically downward and replaces the upper Toolebuc. Ichthyosaurs are common in both formations. As they were usually encased in identical limestone nodules in both formations, and the formations themselves are subdivisions of older stratigraphic groups, provenance is not always clear from data associated with older finds.

The Eromanga Basin had a cool temperate climate in the Aptian and Albian (Day, 1969), and lacked warm-water fauna. It was practically an ichthyosaur feeding-lot, for the arcuate, basin-edge exposures of the Toolebuc Formation and Allaru Mudstone contain most of the world's known remains of Cretaceous ichthyosaurs.

Specimens registered with the prefix QMF are those of Queensland Museum fossil collection, those with prefix MVP belong to the Museum of Victoria, Palaeontology collection. Registered material considered in this paper is listed below.

Holotype QMF2453, Telemon lease, Dunluce Station, via Hughenden. Found in limestone nodules in the shale (Toolebuc Fmn) of the hill halfway between the abandoned Telemon homestead and its abandoned woolshed. Collected, prepared and donated to Queenland Museum by J. Edgar Young. In translating 'one mile from homestead' into 1.6 km from either building, a spuriously exact location is achieved. The spot is not yet relocated.

Paratypes figured or mentioned here, or as *Platypterygius australis* by Wade 1984:

QMF551, Galah Creek, near Hughenden.
QMF3348 (and QMF3389, left wrist and arm only) Stewart Park, Nelia; Toolebuc Fmn.
QMF10686, Boree Park; Toolebuc Fmn.
QMF12314, Kilterry; Allaru Mudstone.
QMF16811, Canary, SE of Boulia, NW Queensland; Toolebuc Fmn.
QMF16812, juvenile within F16811.
QMF13261, Canary, SE of Boulia; Toolebuc Fmn.
QMF12317, near 'Big Hole', Flinders River, near Julia Creek; Toolebuc Fmn.
QMF2299, Brixton, W of Barcaldine, Central Queensland; Allaru Mudstone.
QMF2573, Lydia Downs, Nelia; limestone of either formation.
MVP12989, and associated material numbered P12992, P22653-4, P22656-61. All were numbered 48 by Sutherland; limestone nodule in gypseous shale, Flinders River near O'Connell Creek; Allaru Mudstone.
MVP12991, forefin collected by Sutherland, in 1866, near Flinders River; Allaru Mudstone.
MVP12990, skull fragment collected by Sutherland, in 1866, and numbered 60, Flinders River near O'Connell Creek; Allaru Mudstone.

All specimens but one are from North Queensland; the exception, QMF2299, is the most southeasterly specimen.

We have enough material to establish the intraspecific variability of many bones besides the humeri (Wade, 1984). Acid preparation on the most promising portions of several specimens is still under way, and will probably continue intermittently for years because the longipinnates are not nearly as well known as the latipinnates *Ichthyosaurus* (Sollas, 1916, McGowan, 1973a) and *Ophthalmosaurus* (Appleby, 1956, 1958, 1961). '*Ichthyosaurus* cf. *latifrons*' Watson and Townend (in Romer, 1968) is a species of *Temnodontosaurus* (Appleby, pers. comm.).

Longman (1922) described the Galah Creek skull, QMF551, and had made a restoration sketch of the head in side view. His photographs (his plates 1 and 2) substantiate his complaint that the matrix, which was harder than the bone, could not be removed satisfactorily. His restoration is a classic example of his X-ray vision. He suspected even then that there was no suture dividing the large quadratojugal into lower quadratojugal and higher supratemporal, for he wrote of it with doubt and indicated it only with a faint, dashed straight line. In other respects there is little difference between his restoration and that which Romer (1968) subsequently based upon "*Myopterygius*" *americanus* (Nace), *recte* also *Platypterygius* (McGowan, 1972b). Romer dispensed with the hypothetical suture and the name supratemporal, and showed less curvature in the rear of the lower jaw. In general, Longman's specimen was less damaged than Romer's and he is therefore the more accurate of the two in restoring the jugal, maxilla, pre-narial maxillary foramen, naris and narial crest, even though his artist was less artistic than Romer's. Evidently Longman's work was unknown to Romer in 1968, since Romer was scrupulous about crediting other workers.

The Galah Creek skull has undergone acid preparation (Wade, 1984, fig. 1c; Figs 1, 2), which has been halted lest original articulation be lost. Description of individual bones will depend more on the well-preserved but badly disrupted MVP12989 and other specimens. Essential background to ichthyosaur description is the preservational history.

PRESERVATION

The taphonomic history of ichthyosaurs differs strongly in oxygenated and euxinic environments, and food remains are preserved chiefly or only in the latter. All Australian material to date has been retrieved from oxygenated environments, but when the oil shales near Julia Creek become

economically viable there is hope of well-preserved ichthyosaurs.

Schaeffer (1962) made a prolonged study including taphonomic history of dolphin carcasses in the North Sea and some of its inlets, and suggested (Schaeffer, 1972) that it would be applicable to ichthyosaurs. In part, it is. The North Sea is only slightly less land-locked than was the Albian Australian Eromanga Basin Sea. Both seas were (or are) oxygenated and (at least before netting of the North Sea) teemed with the fish, cephalopods and marine tetrapods of their day. Live marine tetrapods are just negatively buoyant (with turtles as heavy exceptions, and temporary, deep-breathing light exceptions). Relatively few of those that contributed skeletons to the fossil record would have died so rapidly that they escaped death by drowning. Both compression at depth and the weight of water replacing air would have caused the bodies to lie on the sea floor until decomposition had generated enough gas to buoy them up to the surface. Schaeffer recorded the movement of certain carcasses to and fro for weeks or even months; sometimes stranding intervened. Ultimately even connective tissue disintegrated, and the carcasses were reduced to skin-wrapped agglomerations of bones by the time they sank.

The geologist receives skeletons from the fossil record at a stage after they left Schaeffer's jurisdiction. The skin-wrapped bones have lost their binding and are either encased in early-formed calcareous deposits or deformed in more compressible sediments. So far as ichthyosaurs are concerned, two differences stand out from dolphins. First, in ichthyosaurs the jaws had snapped together and had stayed together — unless the connective tissues of the skull had disintegrated — implying that they had a decay-resistant, possibly ligamentous, mechanism for maintaining closure. This observation should be regarded as an extension of the description of musculature by McGowan (1973), not as an alternative. Second, partly- articulated specimens are relatively common in comparison with disarticulated assemblies. Evidently these sank at a somewhat earlier stage of disintegration than many dolphins. Perhaps they were less fatty. The extremities, fin edges and tips, hind limbs and tail fins had usually suffered greatly, and it is normal for little of them to remain. Small-toothed forms, with correspondingly short tooth roots, are gaining a reputation for toothlessness that may be quite undeserved, and may relate to the floating or not floating (below) of the corpses (contrast Appleby, 1956, p. 444, pl. 2, fig. 1, or 1958, pl. IV, with

Martill, 1987a). The teeth, or at least their enamelled portions, were approximately vertical to the jaw (Figs 3A, C) but some sets of jaws show a relative antero-posterior movement which has displaced the interlocked teeth in the tooth grooves of premaxilla/maxilla and dentary as a mass. Alternatively, crushing of the less resistant parts of the skull may displace the more rearward teeth, laterally in QMF551, the Galah Creek skull (Longman, 1922; Wade, 1984). Since tooth loss from the grooves tends to be wholesale when it occurs, toothless ichthyosaurs should not be casually accepted as fact unless atrophied tooth grooves, or an alternative method of feeding, have been demonstrated. The latter possibility has been partly substantiated by McGowan (1979) for one species of *Stenopterygius, S. quadriscissus*, and denied for other species of the genus.

Preservation in euxinic basins is also the preserve of the ichthyosaur and the geologist. Hofmann (1958) traced the effects of taphonomy on the Holzmaden specimens of *Stenopterygius* (Toarcian). These may show current transport or *in situ* breakage, crushing and other deterioration, but many skeletons are essentially complete. Tails terminate in reduced, down-turned tail-fin vertebrae such as are rarely found in oxygenated environments. Fingers and toes taper to tiny phalanges, lateral digits are complete, and fossils of connective tissue surrounds are known. Even some newly born or half-born juveniles lie with their mothers. These are not skeletons of carcasses that have floated for weeks, and many have not floated at all from the place they touched down after death. The Middle Triassic Tessin *Mixosaurus* (Kuhn-Schnyder, 1964) are similarly well-preserved in black shales. Bone-scatter due to flattening is their most common deformation, and stomach contents are commonly represented by fish scales.

Rotting and mineralization are accelerated in euxinic conditions (Allison, 1988). In some iron-rich sediments sulphide decomposition is a problem. The holotype of *Platypterygius platydactylus* Broili (1907) had been excavated and mounted before Broili was able to describe it. The specimen was in part magnificently preserved and in part destroyed by iron sulphide decomposition. The coracoid and parts of some other bones were compressed. Little is known of the upper and inner parts of the skull, but the axial vertebrae are intact except for the proximal 18 or so down-turned vertebrae of the tail fin (Broili, 1907; Wade, 1984) and the tail tip. The pelvic girdle, rear fins, and much of the pectoral fin had deteriorated

completely. In all, it seems to have been a fairly typical case of preservation in an euxinic environment.

NOMENCLATURE

All the specimens here appear to be *Platypterygius 'australis'* (McCoy). The species is caught up in nomenclatural problems because McCoy described it from the first material that came to hand — a few centra, which were not figured and are still at least temporarily lost (Wade, 1984). According to the collector, James Sutherland, the holotype was 'numbered 48 (five vertebral joints)', but McCoy (1867) did not state whether the rib condyles were single (from tail) or double (from body or neck). The measurements he gave do not allow the assumption that the holotype was a close fit to any of the 1866 material (McCoy, 1869) that Sutherland found at the same locality and also numbered 48. This material comprised a poorly articulated skull, with atlas/axis and the next 32 vertebrae in articulation, accompanied by two pairs of larger tail centra (Wade, 1984). These latter might perhaps articulate with the holotype, if it were assumed that McCoy confused height (his 'depth') and width, and if the original piece were found. Unfortunately there is no objective means of relating the holotype to identifiable material, even if it were found and fitted to these tail centra.

Although Etheridge (1888) described a snout fragment (QMF1448) as *Ichthyosaurus marathonensis,* he was inclined to recant and accept it as possibly *I. australis* by the time of Jack and Etheridge (1892, pp. 505-8). The custom of accepting all the material McCoy had handled as the composite holotype of *'I. australis'* arose in Etheridge's day, and Chapman (1914) remarked that *Ichthyosaurus australis* McCoy was 'typically represented by a nearly complete specimen'. This was a strange remark from a worker who had illustrated the smaller remnant of two partial skulls. He figured MVP12990, skull no. 60 of Sutherland's collecting, together with an incomplete forefin MVP12991 which has been separated from its collecting number. From registered data forefin MVP12991 belonged either with skull 48 or skull 60, but the holotype is the five centra nominally described in 1867, and is neither of the two skulls, each with associated material, vaguely discussed en bloc by McCoy in 1869.

McCoy's type description is brief (McCoy, 1867): 'The remains are of the two well-marked genera *Ichthyosaurus* and *Plesiosaurus.* Of the former there are numerous vertebrae, deeply biconcave with conical articular surfaces, the centrum 4 inches wide, 3 inches deep and 1½ inch (sic) long. The species 1 name *Ichthyosaurus australis* (M'Coy).'

The collector and donor, James Sutherland, also mentioned the dimensions 3'' x 4'' in his letter of conveyance to McCoy, though unfortunately he did not specify which was height or width. No (other ?) specimen of Eromanga Basin ichthyosaurs is known to have undamaged vertebrae that are decidedly wider than high (= 'deep'), but it is debatable whether McCoy would have mentioned mild distortion.

If a neotype for *Ichthyosaurus australis* McCoy were to be chosen, partial skull MVP12989 with 34 vertebrae attached, and 4 more associated, would deserve serious consideration. This was found at the type locality only one year after the holotype, and by the same collector. McCoy (1869) made joint mention of this and another specimen under the name *Ichthyosaurus australis,* so the individual has impeccable paper credentials. It lacks fins and humeri and so cannot be distinguished from *Platypterygius hercynicus* (Kuhn) or *P. americanus* (Nace) at a specific level, although the basioccipital is sufficiently close to that of *P. hercynicus* to establish the generic affinity. The skull has a teratologic internasal suture consisting of a row of holes, as its nasal bones were small and met only intermittently in the mid-line. Its bones are well-preserved, though many of them are badly displaced and some are broken. A lower jaw intervenes along the head's median suture, and the two halves of the cranium and rear of the snout are at right angles to each other, the left side being rotated inward. Perhaps because of the aberrant nasals, the nares are small and not easily comparable with other specimens. The base of the basisphenoid is much less flat than the two others known. The latter character may prove to be of doubtful value because Appleby (1961) has emphasized the variability of many of the bones. However, MVP12989 is the most peculiar ichthyosaur skull yet collected in Australia. The probability that it is conspecific as well as congeneric with the remainder of the Australian Cretaceous ichthyosaurs is high, but it is morphologically unsuitable as a neotype for the majority. All the same, any other specimen will always seem a less authentic representative of McCoy's species and of the type locality. In this quandary the future stability of the nomenclature will probably be better served by a new name for the Australian ichthyosaur species most common in the Eromanga Basin; it should be based on the most characteristic material to hand so that it can
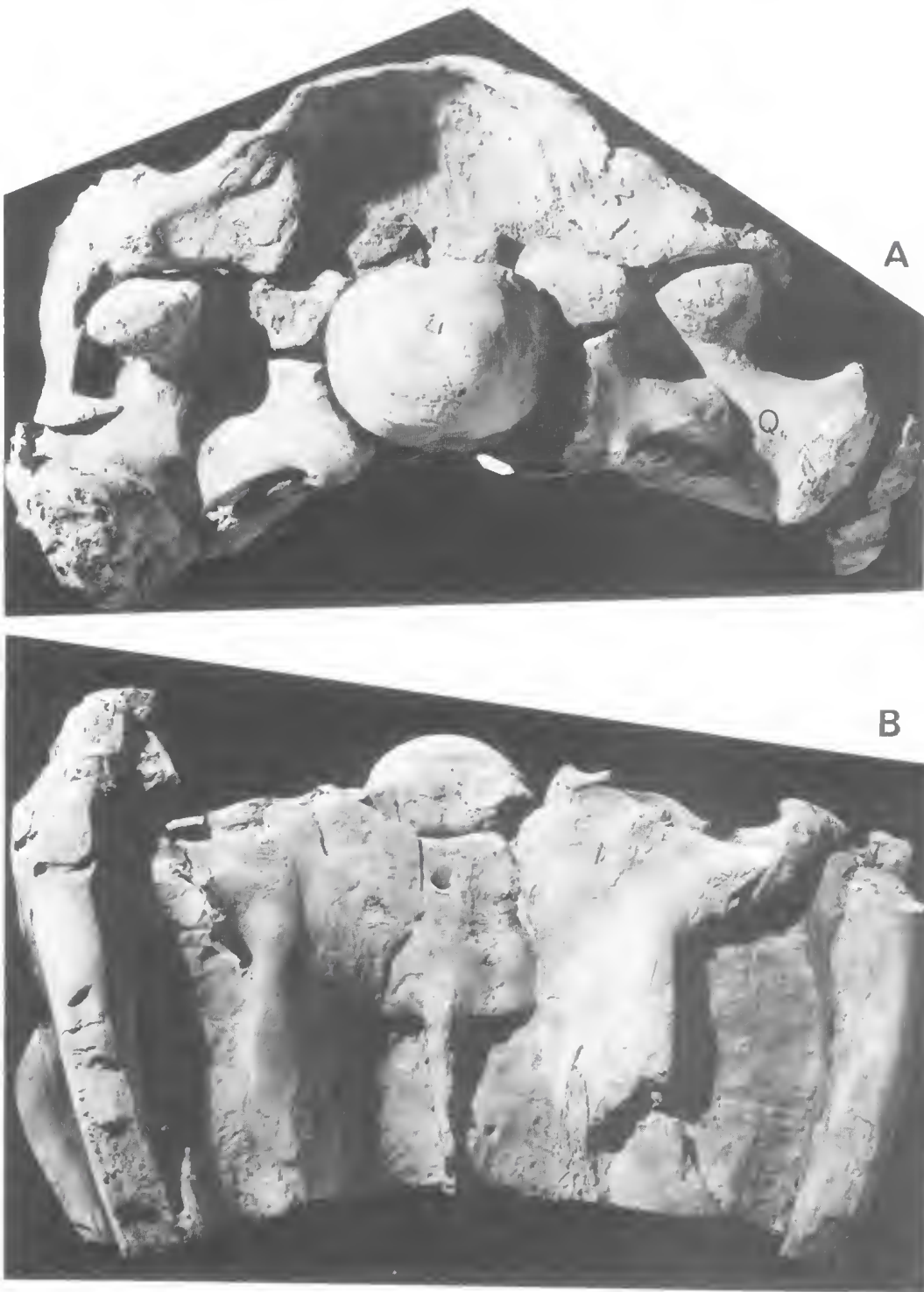
FIG. 1. *Platypterygius longmani* n.sp., paratype F551. A, posterior view of skull. Both exoccipitals have rotated to expose their bases, but have remained side by side; cartilage extended the stapes shaft into the adjacent quadrate socket. Compare Fig. 2B, posterior part of skull in ventral view; right pterygoid and stapes are displaced from basisphenoid and basioccipital respectively. Scale bar = 10 cm.

be specifically determined without reference to other specimens.

SYSTEMATICS

Platypterygius longmani sp. nov.
(Figs 1-6)

? *Ichthyosaurus australis* M'Coy 1867 (indet.).
Ichthyosaurus australis M'Coy 1869.
? *Ichthyosaurus marathonensis* Etheridge 1888 (indet.)
Ichthyosaurus australis McCoy (Jack and Etheridge, 1892).
Ichthyosaurus australis McCoy (Chapman 1914).
Ichthyosaurus australis McCoy (Longman 1922, 1935, 1943).
? *Myopterygius australis* (McCoy) Teichert and Matheson (1944).
Platypterygius australis (McCoy), McGowan, 1972b,c.
Platypterygius australis (McCoy), Wade (1984).
? *Platypterygius australis* (McCoy), Murray (1985).

PROVENANCE

Albian of Eromanga Basin in Queensland: Toolebuc Formation and Allaru Mudstone. The basin also contains ichthyosaur remains in South Australia. *P. longmani* may also be the form known from several specimens, mainly vertebrae,
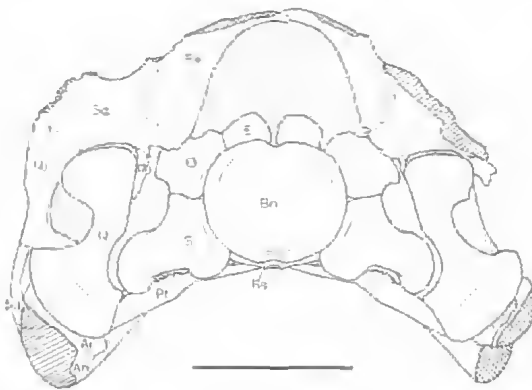

FIG. 2. *Platypterygius longmani* n. sp., paratype QMF551. Sketch of occiput; based on Fig. 1A, but with major displacements corrected. Abbreviations: An, angular; Ar, articular; Bo, basioccipital; Bs, basisphenoid; E, exoccipital; O, opisthotic; Pa, parietal; Pt, pterygoid; Q, quadrate; Qj, quadratojugal; S, stapes; Sa, surangular; Sq, squamosal (dr, descending ramus). Scale bar = 10 cm.

near Darwin, Northern Territory of Australia. These last originate from inner shelf deposits (Murray, 1985) and may indicate the spread of *P. longmani* around the continental shelf.

The foremost worker on Australian ichthyosaurs has been Longman (1922, 1935, 1943), a relative newcomer in comparison to Sutherland, McCoy and Etheridge, but a most percipient worker in many fields. The species is therefore dedicated to him as *Platypterygius longmani* n. sp.

The Galah Creek skull (QMF551, Figs 1, 2) which Longman described in 1922, has no known body so it is necessary to choose the Telemon ichthyosaur, QMF2453 (Longman, 1935, 1943; Wade, 1984) as holotype. This is the nearest to complete Cretaceous specimen on record. It has a good, though obliquely flattened skull (Figs 3A, C), an almost complete axis, many adaxial rib-ends, a damaged pectoral girdle, both humeri (one with wrist articulated) and sundry displaced phalanges (Wade, 1984, figs 1a, b, 2b). Two of several photographs taken during collection by J. Edgar Young, who donated the specimen and photographs to Queensland Museum, attest to the original arrangement of bones in the proximal end of its front fin. McGowan (1972b) accidentally referred his comments on fin structure, not to his copy of a J. Edgar Young photo, but to an arbitrary phalange arrangement that was put together simply for the photograph of the whole specimen. As the arrangement was based roughly on Young's photo, it did correctly have seven digits. It differs in many details from the arrangement now on display, but I regard even this as unauthentic. Another photograph taken by J. Edgar Young, and loaned by Mrs Hazel Young, shows that the snout was 16 cm longer when collected than it is now (compare Figs 3C, 4). The skeletal length, in its discovered state, was given as 18 feet, 5.4 m without the tail fin. The somewhat shorter measure of today, 4.92 m, is probably also due to loss of matrix and obliquity between numbers of tail vertebrae, now individually separate, and aligned vertically. However, it is 11 vertebrae shorter than *P. platydactylus* (Broili) (see p. 128).

DIAGNOSIS

A moderately large, long-snouted ichthyosaur with many strong teeth on premaxilla and maxilla. A pre-narial maxillary foramen which checked the growth of the premaxilla is present, exposing the maxilla, with locally radiating growth, reaching the nasal bone anterior to the naris. Parts of the maxilla may be overlain by superficial flanges of prefrontal, lacrimal and jugal, and premaxilla,
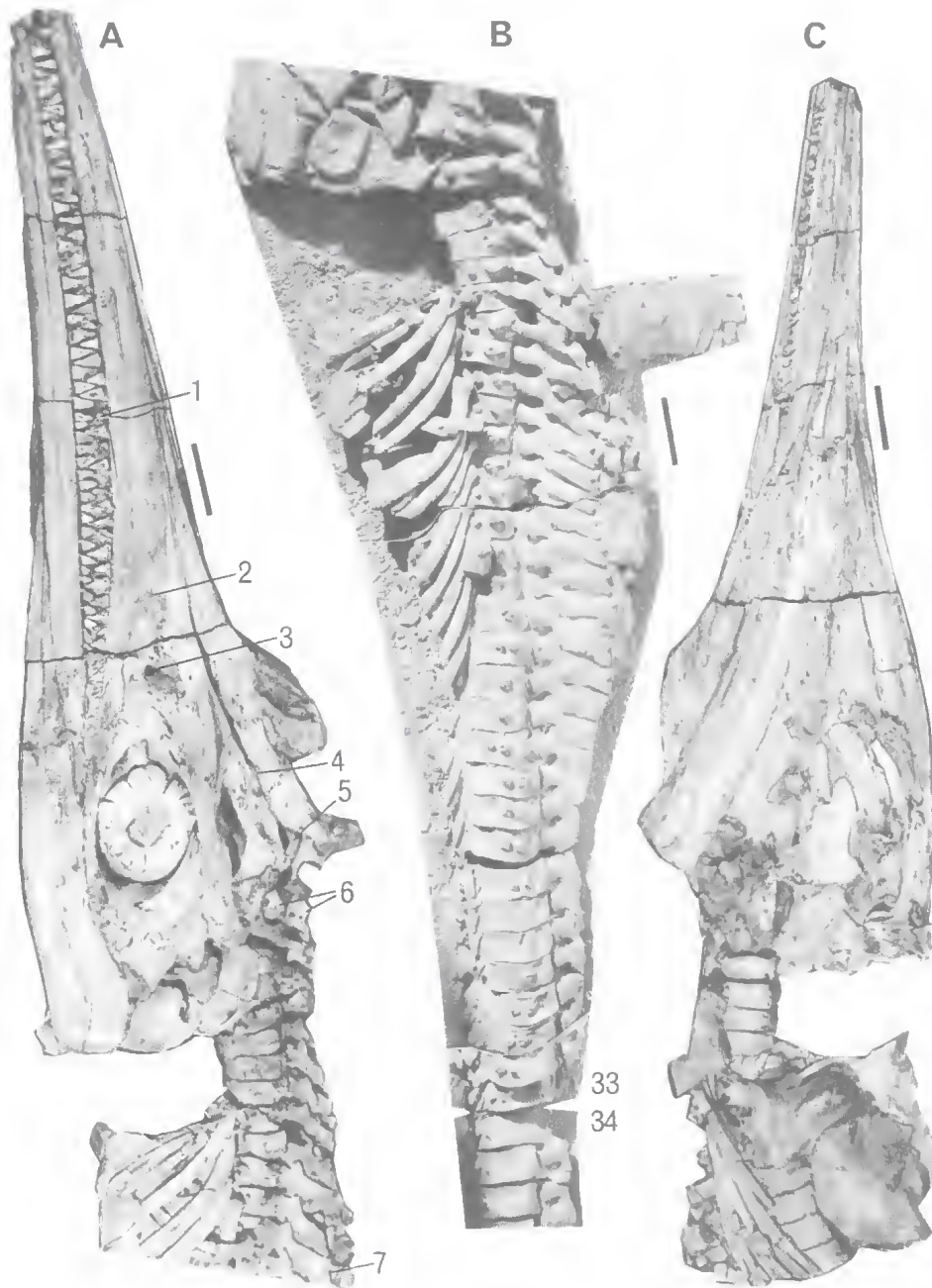
FIG. 3. *Platypterygius longmani* n.sp., holotype, QMF2453. A, skull in left lateral view. Showing 1, anteriormost maxillary tooth; 2, anteronarial maxillary foramen in fork of premaxilla; 3, naris (accidentally enlarged at nasal-maxilla suture during acid preparation; see Longman, 1943); 4, pineal foramen; 5, supraoccipital arch projecting at rear of interparietal suture; 6, exoccipitals (displaced, but have remained together in all three examples where known); 7, V-shaped notch at tip of neural spine in vertebra 11. B, anterior part of vertebral column in left lateral view. Vertebrae 2-32 show reclined articulated neural spines; V-shaped apical notches are evident on neural spines from vertebra 11 to at least vertebra 20 (more posterior spines eroded). Displacement between vertebrae 25 and 26 is an artefact; up to 8 vertebrae may be lacking between vertebrae numbered 33 and (arbitrarily) 34. C, skull in ventral view; left humerus is visible (in slightly skewed dorsal and distal view) between coracoid and scapula fragments. Each scale bar = 10 cm.

FIG. 4. *Platypterygius longmani* n.sp. The holotype (QMF2453) during excavation at Telemon Station, April-May 1935. Skull is exposed in ventral view; three small fragments at tip of snout add approximately 16 cm to measurement of total skull length. Photograph by J. Edgar Young.

around the lower three sides of the nares. The nares are oval to bean-shaped, with a foramen, sometimes accompanied by a crescent of varied fine to coarse perforations, through the nasals above each; the perforations, especially when multiple, help to delineate a narial crest or ridge between them and the dorsal ends of the nares. The orbit is oval in all specimens, and the sclerotic plates form a paraboloid ring thickened at the outer edges; adjacent plates are locked together by a tongue-and-groove structure (like floor-boards). The internasal suture is variable from fully closed to a row of holes (P12989) in different animals (see Wade, 1984, for discussion). The supraoccipital is a high arch of bone enclosing most of the foramen magnum. The paired supraoccipital foramina are anteriorly-opening slots below which the bone expands in antero-lateral wings. The exoccipital facets of the supraoccipital face postero-ventrally, while the impressions of semicircular canals and sacculus face antero-ventrally. Exoccipital/basioccipital facets approach each other to as little as 7 mm apart, the exoccipital shafts draw apart, and their exoccipital/supraoccipital facets draw together again leaving a rear opening to the skull which is more strongly figure-8-shaped than in *Ophthalmosaurus*. The exoccipitals tend to turn back-to-back and stay together, the same way up, when they are displaced. The basioccipital condyle faces almost directly backward. Opisthotic has a large, blocky head and small shaft. Stapes inserted into quadrate laterally and is mesially braced against the basioccipital in a ventro-lateral position (Figs 1, 2). Atlas/axis is heart-shaped in end view, with atlas end appreciably larger in diameter; antero-ventral angle forms a hypapophysis which

is roughened for cartilage articulation. From axis to 32nd vertebra the neural arches are strongly reclined, and the zygapophysial faces meet at approximately $30°$ to horizontal in an antero-dorsal position (Fig. 5). From the holotype, the 11th to 20th neural arches (at least) have the crest of the neural spine divided into anterior and posterior peaks by an asymmetric V-shaped apical notch which is quite broad and slightly rough (as if to attach cartilage). Preservation failures blur the diagnosis toward the posterior. The 21st and subsequent neural arches are progressively more eroded apically, with loss of the notch. From 28th the zygapophysial faces began to approach vertical but were lost as preservation deteriorated. The 46th vertebra present is the first with single rib articulation, but the 33rd and 34th are badly eroded and between them a sudden step in the gradually lowering height of the rib apophyses records loss of centra. Over 45 vertebrae with twin rib-
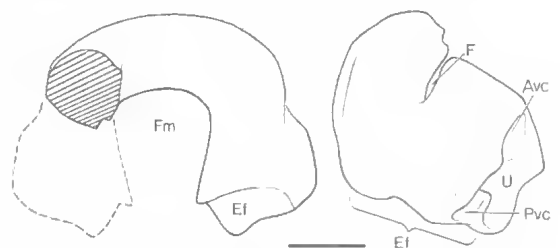

FIG. 5. *Platypterygius longmani* n.sp., paratype MVP12989.Supraoccipital in anterior view (left) and lateral view (right). Abbreviations: Avc, impression of anterior vertical canal; Ef, facet for attachment of exoccipital; F, foraminal slot; Fm, foramen magnum; Pvc, impression of posterior vertical canal; U, impression of utriculus. Scale bar = 2 cm.

articulations, and more than 36 vertebrae with single articulations; tailfin vertebrae are small, but their number is unknown (two collected). Postero-dorsal vertebrae had vertical zygapophyses (caudal arches unknown). Unweathered small tailfin vertebrae have dorso-lateral ridges on either side of the neural groove (QMF12314).

Clavicle adjacent to, but not enclosed by, scapula at any point. Glenoid facet faces laterally when coracoids are undistorted. Femur 0.7 of the length of humerus (QMF10686). Humerus with prominent dorsal and ventral trochanters. Size and shape of pisiform socket and presence or absence of lageniform socket depend on width of distal humeral face compared to total proximal width of radius, ulna, and pisiform; if sufficient space is available, the lageniform (defined p. 129) articulates with humerus.

The three primary fingers lie one below each of radiale, intermedium and ulnare. They are supported by three anterior (radiale) accessory fingers and three posterior (ulnare) accessory fingers. The primary fingers and adjacent first radiale or ulnare accessory fingers form a close-fitted pavement of rectangular phalanges. Phalanges of the more marginal accessory fingers have less regular shapes. The digits increase in length from the anteriormost 3rd radiale accessory (the shortest) to an irregularly-paved tip distal to the most posterior digit (the 3rd ulnare accessory digit). All finblade bones are tightly appressed. The ulnare digit may bifurcate about midlength, to prevent excessive narrowing of the finblade.

DESCRIPTION
Skull

Anterior. The tip of the beak has been preserved in F13261 (paratype from Canary Station, collected and donated by Mr Andrew Robinson). The lower jaw is slightly shorter and shallower than the upper, and its anterior pair of teeth are locked into the 2-3 sockets of the upper jaw. These teeth had been expected to lock into the 1-2 sockets, since the broken snouts of the Galah Creek, Telemon and Stewart Park ichthyosaurs were all a little slighter in the lower jaw than the upper. This occurrence suggests a certain amount of plasticity in the fit of the jaw. Evidently the upper lip would have closed around the edge of the lower, providing a watertight seal when the mouth was closed. The animals still would have needed some sort of throat-valve, equivalent in function to that of a crocodile, to enable the mouth to be opened under water.

Lateral view. Figure 3A has been oriented to give the best possible lateral view of the holotype skull and anterior vertebrae. This skull has been discussed previously (Longman, 1943; Wade, 1984). The maxilla carried 25 teeth and one gap, and the premaxilla 19 plus four gaps and a missing tip previously estimated at 10 cm (Wade, 1984), but now considered 16 cm on photographic evidence (Fig. 4). Sixty teeth per jaw ramus is a conservative estimate.

Although *P. longmani* is quite a large ichthyosaur the naris is small, with an antero-lateral projection of the maxilla rendering it asymmetric, though broadly oval. It is always accompanied by a distinct antero-narial maxillary foramen which caused the premaxilla to fork proximally, preventing it from covering the maxilla anterior to the naris. The forms with horizontally elongate nares (McGowan, 1976) have openings which end anteriorly in a narrow embayment reminiscent of the size and position of the maxillary foramen. It seems possible that as the snout elongated, the elongate naris of primitive form was divided in two by an outgrowth of the maxilla, for its growth pattern radiates in an arc here. This outgrowth isolated the foramen and the surround of the nostrils from one another. The nares are a point of weakness, even at their reduced size, and skulls are usually broken through or close to them.

The strongly ossified sclerotic ring was well described by Longman (1943). At the edge of the inner opening the sclerotic ring is only slightly convex. Outward, the surface describes a short paraboloid. A thick outer margin appears to have offered ample space and surface roughening for muscle attachment. Two areas of great thickening are spaced in the third of a ring which is now free in MVP12989. They suggest four chief adjustor muscle attachment areas within the whole muscle ring. Similar thickening is seen through a chip at the anterior longitudinal diameter in the right eye of QMF3348, the Stewart Park skeleton. The sclerotic plates interlock, with the edge of one plate fitting into a longitudinal groove in the adjacent edge. This tongue-and-groove structure would prevent any movement to change the shape or size, but would have allowed growth and strengthened the paraboloid at the same time. The simple overlap described by McGowan (1973a) for *Ichthyosaurus* would have been less prohibitive of movement than the structure of *Platypterygius*. The latter is closely similar to the structure Watson and Townend (*in* Romer, 1968) figure for '*Ichthyosaurus* cf. *latifrons*', a *Temnodontosaurus*. Claims of mobility in other ichthyosaurs (e.g. *Mixosaurus;*

Dechaseaux, 1955), should be re-examined because mobility would weaken resistance to pressure and seems inherently unlikely. The plates presumably protected the whole ball of the eye from deformation during rapid under-water movements — after all, their possessors usually lived by catching fish and cephalopods, and none of these is likely to have moved slowly. There is no modern sclerotic structure which impinges on the visual operations of an eye, so a very contractile iris, to cope with vast changes in light intensity, should be restored inside the sclerotic ring opening. Human eyes are peculiar in their need to swivel the stereoscopic area, and are a most unsuitable model for the amount of 'white' to be seen around a normal, non-stereoscopic, eye. It is probably correct to fit the ichthyosaur eye with lids and a transparent nictitating membrane, like crocodiles, as the span is unduly large for a thin transparent scale like that of snakes. The skin should cover at least the greater part of the sclerotic ring area (contrast Frey in Reiss, 1986; and Chapman in Taylor, 1987b). The orbit is elliptical, and the proportions of 19.5 cm long to 12.7 cm high, exhibited by the right side of the Stewart Park skull, seem undistorted. Internal diameter of its sclerotic ring is 4.2 cm. Externally the plates curve steeply into the matrix at 12 cm diameter, so that external diameter of the ring must have been close to minimum diameter of the orbit. Anterior-posterior movement of the visual area was likely to be less than its diameter, judging from these ring and socket sizes; it was possibly much less, for the anterior angle of the socket is shallow. The unborn F16812 had an orbital length of 8.5 cm, and skull postnarial length of 16 cm. The snout is broken off at a lower jaw length of 45 cm. Total skull length was probably just over half a metre.

The rear of the skull. This is best preserved in the Galah Creek specimen QMF551 (Longman, 1922; Wade, 1984). Figure 1 shows the occiput as preserved, and Figure 2 shows it reconstructed by correcting for major displacements.

Noteworthy differences from *Ichthyosaurus* and *Ophthalmosaurus* are: first, that the occipital condyle is a greater proportion of the width of the basioccipital (7.3/9.0 cm in QMF551; Figs 1, 2); and, second, its attachment area is not tilted upward posteriorly. The large hammer-shaped adaxial heads of the stapes are braced against the basioccipital antero-laterally and, to a lesser extent, against the basisphenoid postero-laterally. The stapes are separated ventrally by 3-4 cm in different specimens (see Fig. 1B). The cartilaginous lateral end of the stapes was inserted into a postero-lateral

sharp-edged hole (stapes insertion) in the quadrate. Posteriorly the pterygoids (Fig. 1B) have a mesial overlapping contact with the lateral two-fifths of the basisphenoid; they overlap the whole ventral side of the stapes shaft, and the quadrate shaft external to the stapes insertion. This massive line-up of bones appears, from size and orientation, likely to have taken as much of the stress of quadrate-articular joint movements as the upper quadrate shaft leading to the squamosal, and braced by the quadratojugal. The opisthotic-stapes contact is at the horizontal diameter of the basioccipital (Figs 1, 2), so that the stapes facet is ventro-lateral and the opisthotic facet dorso-lateral on the basioccipital. The opisthotic-basioccipital contact is flat and, like all the basioccipital contacts, apparently had cartilaginous surfaces on both sides. Laterally, the opisthotic contacts the squamosal close to the head of the quadrate, but is separated from the quadrate by a descending ramus of the squamosal. The quadrate is very similar to that of *Ophthalmosaurus* (Appleby, 1956, fig. 7). The quadrate can be described as approximately harp-shaped, if the articular facet and neighbouring thick portion of the quadrate shaft is compared to the foot and resonating box, from which both "posts" arise, with a thinner fan-shaped area between them. The stronger, longer "post" terminates in the quadrate-squamosal facets, its main facet being terminal and its minor facets at the outer edge (Figs 1, 2). The shape of the main head is a large sector of a circle; in MVP12989, the only quadrate freed of matrix, it is a 90° sector, while in QMF551 it is broader, but not fully exposed. From the centre, and extending out from the more mesial radial face, the thinner, fan-shaped portion of the quadrate describes an arc forward and downward to the top of the shorter, anterior "post". This tapers as it curves up from the articular facet, until it terminates as only a slight broadening of the anterior side of the fan. The whole arcuate fan is topped by a groove, roughened for cartilage attachment, and depressed between sharp edges, as described for *Ophthalmosaurus* by Appleby (1956). The curve of the anterior 'post' delineates Appleby's 'anterior notch of the quadrate', and the postero-lateral curve of the posterior 'post', his 'posterior notch of the quadrate'.

The dorso-lateral quadrate head is set into a stout socket of the squamosal bone, which makes up the rear outer corner of the temporal fossa and, indeed, the whole thickness of its rear wall. The rear wall extends further ventrally on the inside of the socket than the outside. The grain of the bone radiates in

every possible direction from the centre of the socket, and this grain carries through to the extreme tip of a strong ramus of bone directed downward and anteriorly between the quadrate head and the opisthotic head. Figures 1 and 2 show more of its rear edge on the left side than right. The parietal adjoins the squamosal on the rear of the skull, superficial or mesial to the opisthotic socket, and either bone may lie against the short opisthotic shaft laterally. The parietal forks into a short branch which forms the base of the posterior arch of the skull roof, and a longer antero-mesial branch with its mesial surface directed against the blocky opisthotic head, while its opposite face is applied to the descending ramus of the squamosal, wrapping around its mesial and anterior sides. The descending ramus is the longer, and also lies against the opisthotic head. The squamosal and parietal thus make a contact parallel to the opisthotic/basioccipital facet, and complete the stabilization of the basioccipital.

The descending ramus of the squamosal (in VMP12989) thickens anteriorly and passes down from the body of the squamosal to form much of the posterior and lateral walls of the temporal fossa. It extends through the embrace of the anteromesial flange of the parietal, and more ventrally forms a long, wide, tapered plate joint with an ascending ramus which is welded to the pterygoid. This ascending ramus probably originated from a separate centre of ossification. The descending ramus shows the striations of the main squamosal ossification pattern on its face, which is also slightly fluted. These minor and major elevated structures meet complementary depressed and raised structures on the tapering ascending ramus, so that the joint must have been immovable in life. The ascending ramus articulation naturally faces mesially to complement the outer face of the squamosal's descending ramus.

Antero-ventrally, the mesial angle between the ascending ramus and the pterygoid proper accommodated the basipterygoid process of the basisphenoid in a sharp-edged socket. Thus the ascending and descending rami make a solid shaft extending from basipterygoid process to the rear of the temporal fossa. Watson and Townend (1968, fig. 9A left) very clearly figure a connection between the quadrate wing of the pterygoid and the descending lamella (ramus) of the squamosal in *Temnodontosaurus* sp. (= "*Ichthyosaurus* cf. *latifrons*") as well as an epipterygoid. McGowan (1973) more lately described two structures arising from the pterygoid. He did not join the 'quadrate wing' to the descending ramus of the squamosal but discussed its fit against the side of the quadrate — although he figured the ramus (1973, fig. 46) partly between the quadrate and the 'quadrate wing'. *Platypterygius* is relatively short in comparison to height and width in its basisphenoid length. It is not possible by looking at *Platypterygius* to judge the accuracy of the several reconstructions of this area in forms with a greater proportionate basisphenoid length. What is clear is that here one structure is occupying the place and function which historically have been assigned to two. The cartilage edge of the quadrate fan, here, seems to have been practically median in the temporal fossa rear base, and to have been directed upward and anteriorly.

The matrix-free bones used here are those of MVP12989, but they receive abundant confirmation from QMF2453 and QMF551; only the ascending and descending rami and basisphenoid/basioccipital contact depend wholly on VMP12989. This was used for etching because the bones were in very good condition, though displaced sufficiently to require refitting. Laterally the inwardly flaring quadratojugal foot rests on the dorsal edge of the outwardly flaring part of the quadrate foot, and the laterally flat quadratojugal shaft rises to meet the squamosal, just outside the head of the quadrate (Figs 1, 2).

The parietal arch is higher than a semicircle, and encloses the high arch of the supraoccipital (*vide* QMF2453 and MVP12989) which rests on the exoccipitals and encircles at least three-quarters of the foramen magnum. The foramen magnum and the space between the exoccipitals are combined in the fossil as a single figure-8-shaped space. The parietal may overlap on the squamosal in the rear suture, (*vide* QMF551) although the opposite overlap occurs here in the parietal-squamosal crest; as a result flanges of the parietal lie over the squamosal above and behind the upper half of the opisthotic-squamosal contact. They interdigitate in MVP12989. Inside the temporal fossa of QMF551, the squamosal-parietal suture picks its way down the middle of the rear wall of the temporal fossa, squamosal overlying parietal. This suture can also appear in the usual position in which it is recorded, in the inner posterior corner of the temporal fossa. The ventrolateral-anterior wings of the supraoccipital (Fig. 5), the opisthotics and the prootics all carry the impressions of two semicircular canals and the adjacent parts of the utriculus or sacculus, but except for the supraoccipital, these bones are not yet clear of matrix, and the arrangements of the ear must await later description. Every word which McGowan (1973a) said about the lack of directional hearing
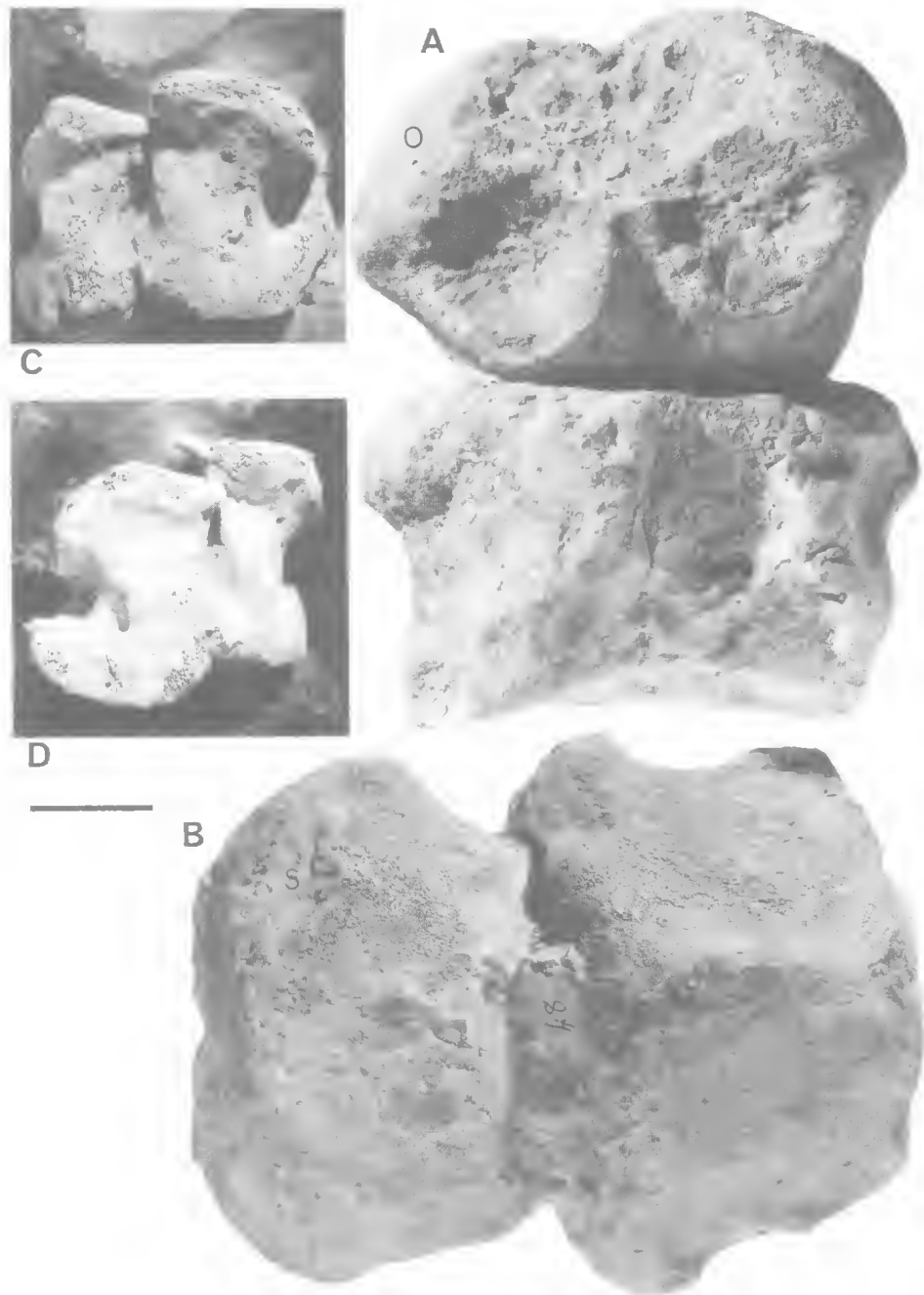
FIG. 6. *Platypterygius longmani* n.sp., paratype MVP12989. A, basioccipital and atlas/axis in dorsal view; showing neural canal furrow terminating as a small tapered depression less than half-way across the basioccipital. The furrow is flanked by large scars for attachment of exoccipitals; anterior to tip of the furrow is a pair of larger medially-contiguous depressions for the hind brain. Facet for opisthotic (O) is situated antero-medially. Floor of neural canal is damaged on axis. B, basioccipital and atlas/axis in ventral view; showing hypapophyseal facet on atlas, and stapes facet (S). C, D, two views of the paired exoccipitals; despite major displacement the two bones have remained in close association. Scale bar = 2 cm.

of ichthyosaur ears receives support from these bones. The huge semicircular canals bespeak specialization for balance, which was needed, for they were rapid, agile movers in a uniform milieu, and could not rely on their eyes and feet to relate them to a substrate, like land-dwelling reptiles. Directional vibrations may have been detected in the skin, rather than the ear.

The supraoccipital (Fig. 5) resembles that in *Ophthalmosaurus* (Appleby, 1956, 1958) but curves in more at its feet, as the exoccipital facets are close together. The foramen terminates at the height of the dorsal corner of the lymphatic foramina which are such a distinctive feature of the latipinnate supraoccipitals (Appleby, 1956, 1958; McGowan, 1973a). *Temnodontosaurus* sp., a Liassic longipinnate, had fully enclosed foramina (Watson & Townend, *in* Romer, 1968). Appleby (letter dated 3rd October, 1988) tells me that he has a Lower Hauterivian *Platypterygius* to describe, with these foramina encircled by bone. Here a pair of foraminal slots, open anteriorly, represent these foramina, and tend to separate antero-lateral wings from the main arch enclosing most of the foramen magnum (Fig. 5). This arch rises from postero-ventral sockets holding the upper exoccipital facets. Exoccipitals are easily displaced *as pairs* (three examples) but tend to turn back to back (two of the three). No single exoccipitals have been found. From this it is assumed that the exoccipitals were both joined posteriorly to the same sheet of connective tissue, and only the supraoccipital enclosed the functional foramen for the nerve cord. The exoccipitals closed to 8 mm apart at their bases in VMP12989 and 1 cm in QMF551, unlike *Ichthyosaurus* exoccipitals; basally they walled only an inwardly and upwardly tapering relic of the wide channel for the axial nerve cord which is found on the atlas/axis (Fig. 6A) and other vertebrae. The nerve cord had thus begun to turn from horizontal toward dorsal as it crossed the junction of atlas and occipital condyle, thus avoiding potential stress at the mobile joint. It also results in a steeply-dipping hind brain to bring the 12th nerve to its exoccipital foramina. This contortion is apparently a better solution to the relative shortening of the cranium than to telescope the hind brain. The basisphenoid-basioccipital contact sloped at 50° to 60° to the horizontal, but if the basioccipital condyle is excluded, the basioccipital is about twice as long dorsally as ventrally. The result is very little up-slope on the occipital condyle. That the occipital condyle of *Platypterygius* is correctly oriented to take an almost horizontal vertebral column is confirmed by

Figure 1B, because any attempt to tilt upward the basioccipital and basisphenoid would bring the long parasphenoid down against the tongue. The exposed length of the parasphenoid projects 24 cm beyond the basisphenoid. It takes origin from below a wide, shallow pit floored by the antero-ventral edge of the basisphenoid, but over-grew it adposteriorly, almost to the posterior carotid foramen. Anteriorly, the carotid foramen is dumbell-shaped in P12989, and lies just above this pituitary pit (Watson & Townend *in* Romer, 1968).

Axis

In numbering vertebrae the fused atlas/axis is counted as two, here, and by most authors. Length, width and height are measured parallel to these dimensions of the animal.

The atlas/axis is almost heart-shaped in end view. In the Kilterry specimen (QMF12314) and MVP12989 its ventral angle is just under 90°. As usual there is one high-set rib condyle, vertically elongate, on the atlas and two equidimensional condyles on the axis. The greater diameter of the atlas end produces a ventro-anterior ridge, almost a keel, on the front half of the fused vertebrae. This (Fig. 5) is sculptured anteriorly for cartilage, and is a hypapophysial facet.

Interestingly, the straight Telemon axial skeleton is very similar to the '(a) type with straight tail without elongated neural spines in the tail' of Riess (1986, p. 102). The chief exemplar of this '(a) type' is *Shonisaurus* with a concave basioccipital condyle, convex atlas, and paired condyles on the zygapophyses. His second (convergent) example is *Eurhinosaurus*. In *Platypterygius* the zygapophysial condyles are single; the prezygapophysis is set on a slight, anteriorly concave pedestal, and the postzygapophysis in neural arches 2-30, is part of a backward slope from the top of a similar, less concave rear to the arch. It is sloped 30° in antero-dorsal vertebrae, steepening from 28-32 onward. In QMF2453 the neural spines, posterior to the neck, have increased in length and height until spine 20, at which point they become progressively more eroded dorsally but still increase in length for another 10-12 vertebrae, until indications of height and finally shape are lost (Fig. 3B). However, the complete to almost-complete spines 11-20 each have a broad V-shaped re-entrant in their apices, rising to short peaks anteriorly and posteriorly. The posterior peak is the longer, though height seems constant. These re-entrants are wholly in quite thick bone, sometimes with a slight border (Fig. 3A, vertebra

11; Fig. 3B, vertebrae 11-20). They provided adhesive surfaces presumably for cartilage, rather than connective tissue, as the articulating surface was quite broad. Ligaments are less likely, as the facet does not thin in the V. It is impossible to observe the posterior extent of these structures, but after vertebra 32 (and several missing vertebrae after the eroded 33) the neural spines probably cease to be raked backward, and the zygapophyses are re-aligned toward vertical. It is tempting to assume that the rearward slope and successive overlap of neural spines 11 to 20+, and their notched apices, indicate the position of a dorsal fin, strengthened by a median row of cartilages. If so, it is more anterior than that attributed to *Stenopterygius*, in the position of the dorsal fin of *Orca*. Though probably the upslope would have been raked backward as steeply as the neural spines, the posterior edge is an utter unknown which may have overhung at 50-60° (vertebrae 28-31) or been filled in. There is a hint of similar apical notches to be seen in the figure of the most oblique spines on antero-dorsal vertebrae of *Ichthyosaurus conybearei* Lydekker (McGowan, 1974b, fig. 9, holotype, BMNH 38423). But the structure should have been described already if it is common.

The axis, like the following vertebrae, has two rib apophyses, the higher touching the base of the neural arch. The succeeding conditions are: vertebrae 3-13 cervical and front antero-dorsal vertebrae with the upper condyle touching the base of the neural arches; 10-30, rib condyles gradationally eased away from neural arch and descended slowly from 'touching neural arch' to lateral; 34-45, postero-dorsal vertebrae with both rib condyles positioned ventro-laterally. (Severe weathering of the right sides of 33/34 suggests that these were exposed at discovery. The loss of vertebrae here is indicated by greater subsequent distance between neural arch and upper rib condyle, and the fact that the change-over to single rib condyles occurred at at vertebra 54 in Broili's *P. platydactylus* — eight vertebrae more than holotype *P. longmani*). Vertebra 46 has a long, vertical single rib apophysis, and thereafter the apophyses are single and rounded. Other examples of the change-over to single apophyses show that they may be single and long on one side of the vertebra while still double on the other; this is the case in one of a sequence of the three largest vertebrae in our collections, found loose and without identifiable material, from Yam Bore Creek, QMF16791a-c). These specimens were scattered and lay flat, and have been greatly

compressed longitudinally to about 4 cm long. Height at centre dorsal to base 13.4 cm (two specimens). Shape oblate, widest below centre, 13 and 14 cm, rather distorted (same two vertebrae). In this position the height of the edges of the neural groove is lost, but this measurement can be used on abraded material. In fact, the vertebrae are all higher than wide, by inclusive measurement.

Lateral displacement of the rear of the Telemon skeleton by 1-2 m, is shown in a collecting photograph by J. Edgar Young. The quality of preservation has deteriorated posteriorly, and since collection the original sequence of vertebrae has been disordered. A few poorly preserved vertebrae may be wrongly positioned still. Vertebrae may be missing after 78, where there is a sudden diminution in size in 79-81, but *P. platydactylus* (Broili, 1907, pl. 12) shows a similar diminution in 91, 92; it may indicate enclosure in the base of the tail fin. *P. longmani* 82 and 83 are diminutive from the tail down-turn. The Telemon specimen thus has 11 fewer vertebrae preserved in the horizontal axis than the holotype *P. platydactylus,* but its axis was broken in two. Restoring the eight vertebrae less than *P. platydactylus* to the eroded mid-dorsal region would add 36 cm to the length between the rear of the dorsal fin and the pelvic fins; restoration of the remaining three vertebrae less, close before the tail bend, would add 6 cm or a little more there, so that the probable dimensions of *P. longmani* holotype become: head, 1.49 m (see Fig. 4); atlas/axis to last double-headed ribs 2.52 m; single-headed ribs 1.43 m. Axial length, 5.44 m plus tail fin; total length under or over 6 m, depending on the adjustment of the tail bend.

The distal tail vertebrae of QMF2453 rarely show rib apophyses because of largely chemical erosion (they were outside the calcareous nodules), but it is possible to trace the bases of rib condyles in a low lateral position, instead of ventro-lateral, at and just after 66. The redistribution of muscle mass in the rear tail that Appleby (1979) described, presumably took place here too. The very high position of the cervical rib attachments (and adjacent anterodorsals) bespeaks the powerful neck musculature used in diving.

The two tail fin vertebrae 82 and 83 resemble those of Broili (1907, figs 2, 3) except in their poor preservation; more were scattered among the Kilterry skeleton, QMF12314. These last are very well-preserved, and have the dorso-lateral portions drawn up into smooth longitudinal ridges on either side of the neural canal; they are distinctly higher than wide, with anterior rim larger than the posterior rim, and a narrower waist. The general

shape is thus not the cotton-reel shape made known by Broili (1907), though many of his may have been stuck down by the dorsal side. His mentioned faint trace of the neural cord is not figured.

The fore fins and coracoids were described by Wade (1984).

In terms of most ratios and characters tabled by Mazin (1981) for *Grippia*, 'Mixosaures', Liassic latipinnates and Liassic longipinnates, the holotype *P. longmani* (or, where marked *, QMF10686) yield: 2, premaxillary segment/mandible = 0.44; 3, prenarial length/mandible = 0.65; 4, longitudinal diameter orbit/skull postnarial (same plane) = 0.58; 5, longitudinal diameter orbit/mandible = 0.15; 6, internal diameter sclerotic ring/longitudinal diameter orbit = 0.26; 7, length naris/longitudinal diameter orbit = 0.14; 9*, max. width pectoral fin/length pectoral fin = 0.48; 11*, length femur/length humerus (both crushed) 0.7; 12, distal breadth humerus/length humerus = 0.73 (to 0.85 in broad humeri); 14, number maxillary teeth = 26; 15, number primary fingers in pectoral fin = 3; 16*, total fingers = 9; 17*, phalanges in longest finger = 37 (including fin-tip phalanges which are not really aligned in fingers, though the pavement tip recurves to terminate below the last digit, ulnare accessory digit 3).

COMPARISONS

Skeletons of other Cretaceous ichthyosaurs are rare, and not adequately described except for *Platypterygius platydactylus* (type species) and *P. hercynicus* Kuhn, 1946. McGowan (1972b) has mentioned considerable skeletal material with *P. americanus* (Nace) but only added description of proximal portions of pectoral fins to the redescription of the skull by Romer (1968). Kiprijanoff (1881) described scattered bones of various sizes in his brilliant monograph. His material is now known as *Platypterygius kiprijanoffi* (Romer), or by the older species name bestowed by Kiprijanoff, *P. campylodon* (Nesov *et al.*, 1988).

Wade (1984) indicated that the particular four-bone-wide forearm of *Platypterygius* was a generic character, and the attachment or lack of attachment of the sesamoid bones to the humerus was presumably of specific value, as it was localized in geographic distribution and/or time. After discussion with Appleby on the fact that the sesamoid bones on the ulnar side were the best attached in *P. 'australis'* while the flask-shaped bones of the radial sides were best attached in *P. americanus* (McGowan, 1972b, pl. 1), Appleby

suggested the employment of the term lageniform for the radial accessory bone. The use of pisiform and lageniform appeals to me as a better solution than trying to dispense with the established name pisiform for the ulnar accessory. It also recalls the constancy of the general shape McGowan (1972b) described. The pisiform of *P. longmani* always, and the lageniform sometimes, was articulated to the humerus. In *P. hercynicus* Kuhn (1946, pl. 1, figs 4, 5; pl. 3, figs 5, 6) the left-fin pisiform and lageniform appear to be in small sockets, while in the right fin they appear merely to lip against the distal corners of the humerus. The left humerus is shortened by compression and, as far as the figure shows, pressure could have achieved the result. However there is no need to rely on sockets to differentiate the humerus of *P. hercynicus*, since this is done by the immense dorsal trochanter. *P. kiprijanoffi* (Romer) lacks both pisiform and lageniform socket, but its radial humeral edge is squarer than its ulnar edge (Kiprijanoff, 1881, pl. 14, figs 1, 2), so presumably it is closer to *P. americanus* and even *P. hercynicus* than to *P. longmani* and *P. platydactylus*. It remains to be seen whether whole fins will bear out the hints obtained from the humeri.

Kiprijanoff (1881, pl. 9, fig. 1) and Romer (1968, figs. 2, 3) restored their ichthyosaur skulls with elongate nostrils against which the premaxilla forks. Both were damaged in this region, and the restorations may owe much to restorations of other ichthyosaurs. *P. platydactylus* and *P. hercynicus* figured material can add no data comparable with the *P. longmani* naris.

P. longmani and, as Krapf (in Broili, 1907, pl. 12) figured serially diminishing phalanges on the leading finger, possibly *P. platydactylus*, have a short leading-edge finger to their fins, but only *P. longmani* has a near-complete fin blade. In this the remaining accessory and primary fingers are serially terminated so that the front edge of the fin-blade skeleton is reclined all the way to its tip. *Eurhinosaurus huenei* has a similar digit arrangement but it is not described from *Excalibosaurus costini* McGowan (1986, fig. 1a), the apparent ancestor of *Eurhinosaurus*, and convergence is likely. *P. americanus* has no complete fin blades described, but has no larger proportion of dorsal trochanter to humeral shaft than *P. longmani* and *P. platydactylus*. *P. hercynicus* Kuhn has coupled its immense dorsal trochanter with full-length primary and secondary fingers (Kuhn, 1946, pl. 3, figs 5, 6). Both pisiform and lageniform lip against the edges of the humerus, but have little or no room to socket there.

The broad expanse of bone near the outer tip of the fin seems reason enough for the exceptional dorsal trochanter, as the animal cannot have avoided the necessity to control much more leverage than the tapered fins exerted. The array of occipital bones is practically identical in Kuhn's figures and *P. longmani*, though less complete in *P. hercynicus*.

From these comparisons and observations it is possible to conclude that the rear of the skull is important for major differentiation, even when there is a degree of convergence (*Ophthalmosaurus* is more like *Platypterygius* in rear-end proportions than the earlier *Ichthyosaurus* is), but the total pectoral fin is the more sensitive structure at specific level.

CLASSIFICATION IN RELATION TO *PLATYPTERYGIUS*

The descent of ichthyosaurs is very incompletely known. Either the fossils or the descriptions of earlier ichthyosaurs and ichthyosaur-like animals are lacking. Their described history begins in the Middle Triassic, with two forms that are at least ordinally distinct: Mixosauria Appleby, 1979, and Ichthyosauria Jaeger, 1824. Appleby (1979) divided the Ichthyopterygia into four 'orders' — Mixosauroidea, Longipinnatoidea, Heteropinnatoidea and Latipinnatoidea. Mixosauroidea were distinguished from the other three taxa by many characters of the axial column including tail fin, girdles and limbs, as well as teeth and proportions of the head; in the other three 'orders' the differences were of proportion, paired fin structure and degree of reduction of the pelvic girdle. A major two-fold division of these ichthyosaurs is thus implied by the data, and was used by Mazin (1983) in the form Mixosauria and Ichthyosauria and is followed here. Longipinnates, heteropinnates and latipinnates are subordinate to Ichthyosauria.

The classification of ichthyosaurs is going through a period of disarray. On the one hand Appleby is working on a morphologic/stratigraphic basis designed to uncover evolutionary trends, and on the other Mazin (1983) has started, and Riess (1986) has 'simplified', a cladistic analysis in which the plesiomorphy or apomorphy of a number of basic characters is very suspect. For example: Mixosauria and Ichthyosauria had most of their skull joints formed by overlapping bones bound by connective tissue in life; the median longitudinal suture of the snout is smooth and vertical. The snout was thus capable of passive displacement, in response for example to biting on a belemnite guard or a stout bone with only left or right jaws. McGowan (1973) has

carefully considered and rejected the idea of a fully kinetic skull. The pineal organ penetrates the skull posterior to the snout as in other Ichthyosauria, usually through the fronto-parietal suture and above the orbits. In *Grippia* (Mazin, 1981) it is wholly parietal and above the rear of the orbits. The nasals were not elongated, so the nostrils were relatively and absolutely close together, more dorsal than lateral, enclosed between nasals and maxilla, and superficially, the premaxilla. *Grippia* thus has a more primitive narial position than any other described ichthyosaur, and Mazin was probably correct in assigning it to a sister-group of the immediate ichthyosaur ancestor. It seems unlikely that the ancestral dentition was specialized for shell-crushing as that would have inhibited the development of passively displaceable snouts, a constant character of all other ichthyosaurs, and probably of the mutual ancestor, as the premaxillae to nasals of *Grippia* tended to split along a straight median suture (Mazin, 1981, fig. 3). In *Grippia* the maxillary teeth were not just short expanded cones, but had started to form a pavement, an irregular double line (Mazin, 1981, fig. 7a). Mazin (1981, figs 3, 4) shows two specimens in which, despite flattening, the frontal to parietal portion of the median suture does not open like the premaxilla-nasal portion or the rear of the parietals. Dechaseaux (1955) has figured slightly modified rear maxillary teeth on *Mixosaurus* and Mazin discusses them; these are probably more like the ancestral condition than the double line in *Grippia*. The order Ichthyosauria had isodont teeth.

A tooth-density index that depended on teeth counted in the central 10% of the snout was utilized by McGowan (1976). His objective care in counting teeth present in a fossil, and excluding any gaps from consideration, brings this ratio under doubt. McGowan (1976) found 14 teeth on the maxilla of *Platypterygius americanus*, where, in the same individual (University of Wyoming 2421) Romer (1968) found teeth and gaps enough to restore 22. The Telemon *P. longmani* (Fig. 3A) has 25 teeth + 1 gap on the maxilla, about 60 teeth in each of its four jaw rami. In confining himself to measureable or countable skull characters, McGowan (1976) related, at 'logical' familial level '*Leptopterygius*' *acutirostris* and *Mixosaurus cornalianus* among others. The generic placement of *acutirostris* is fluid: McGowan (1976) changed the assignment to *Temnodontosaurus* in a footnote and back to *Leptopterygius* in 1979 (in a paper in which he referred to his 1976 paper). Mazin (1983) uses a placement in *Stenopterygius* in the table quoted by

Riess (1985), and Appleby recommended placement in *Temnodontosaurus*. The measurements used by McGowan (1976) for multivariate characters are repeatably defined, but that is not enough to make them taxonomically significant; it is necessary to know what is being measured — the feeding guild to which an animal belongs (Massare, 1987) or its relationships? Tooth-size is normally correlated with the height of the jaw (a fair measure of the jaw's strength) and both are related to diet and the feeding method. Appleby's (1979) use of a post-narial length to form a ratio with orbital length is a distinct improvement on a ratio of orbital length and jaw length, since it eliminates snout length — the most variable quantity in closely-related ichthyosaurs, and one most likely to be responsive to hunting technique and prey. For other proportions Appleby used ratios of single bone measurements, which eliminate the compounding or minimization of variation that can arise sporadically when measurements are spread over several bones. Although it is necessary to be conscious of gaps in our knowledge of occurrences, Appleby's technique of plotting comparative measurements in morphologically related groups against time is very informative of trends.

Appleby (1979) showed that a distinctive style of fin-broadening with the introduction of a mid-fin digit distal to the wrist gave rise to animals with heteropinnate fins, as distinct from those with longipinnate fins. Further acceleration brought the digit head into the distal carpal row, as *Protoichthyosaurus prostaxalis* gave way to *Ichthyosaurus intermedius,* and so animals with heteropinnate fins gave rise to those with latipinnate fins. The single-bone proportions he gave substantiate his fin-sketches, and it is possible by means of them to recognize the Rhaetic *Temnodontosaurus tenuirostris,* which can be described as the first longipinnate at present known to have broadened its fins, as a forerunner in the heteropinnate lineage.

This style of fin-broadening was characterized chiefly by the introduction and acceleration of the mid-fin accessory digit, either single or subsequently forked, to a longipinnate plan. The mid-fin accessory digit terminated proximally either in the metacarpal row or often in the distal carpal row (as a twin bone to the centrale). This second centrale has been widely accepted as a primary wrist bone *because of its contacts* but its derivation becomes glaringly obvious if the midfin accessory digit is picked out in a number of illustrations of the earliest Jurassic heteropinnate

and latipinnate fins; those corresponding to the names *Protoichthyosaurus prostaxalis* (Appleby 1979), *Ichthyosaurus intermedius* Conybeare and *Ichthyosaurus communis* Conybeare (Appleby, 1979; and, for example, McGowan, 1974b). Accessory digits were often added laterally, but the lineage retained acceleration in the midfin as a tendency, and occasionally the intermedium was fitted into the forearm between the radius and ulna.

The problem of inadequate preparation bedevils ichthyosaur taxonomy even when workers know what to look for, and have access to appropriate material. For example, McGowan (1979) was able to see the basioccipital of *Stenopterygius* in full three dimensions in only one example of an isolated bone, 'possibly' of *Stenopterygius,* in his all-embracing investigation of German Lower Jurassic ichthyosaurs. Parts of the two lineages are clear: the extended heteropinnate to latipinnate lineage which Appleby (1979) established — starting with '*Leptopterygius*' *tenuirostris* (which he later informed me was a *Temnodontosaurus)* — and the very short *Excalibosaurus-Eurhinosaurus* lineage which McGowan (1986) suggested could have arisen from '*Ichthyosaurus tenuirostris*'. After all the work on *Stenopterygius,* our most common ichthyosaur, the intractable beast still has no obvious close relatives. Its fused ischiopubis is a barrier to an ancestral position in relation to *Platypterygius* unless and until ischiopubes are discovered there. Its forefin is marginally longipinnate but shows considerable irregularity, including interdigit rows of small sesamoid bones (Johnson, 1979). What is known of the basioccipital is shared by primitive and latipinnate ichthyosaurs, and is unlike *Platypterygius.* The dorsal fin of *Platypterygius* was probably well forward of that in *Stenopterygius.* It would be interesting to know whether *Stenopterygius* had the same pterygoid-squamosal rami as *Platypterygius.* The isolated skull *Grendellus* is a potential platypterygiid, as McGowan suspected from the first, but its basioccipital is still "on the way" to that of *Platypterygius.* While Appleby has informed me that Watson and Townend (1968) were studying a *Temnodontosaurus* sp., their specimen has the elongate basisphenoid-basioccipital with basioccipital peg seen also in *Ichthyosaurus* (Appleby, 1961), and McGowan (1979) states that *Temnodontosaurus platyodon* has no such peg. In short, two to four lineages are being attributed to temnodontosaurid ancestry, which is possible, since species do not interbreed, but messy for taxonomy. More probably, differentiation of the Ichthyosauria had not

proceeded beyond about family level when the group died out.

The style of fin broadening that led to *Platypterygius* was free of advanced midfin accessory digits, although the only near-complete fin has doubling of one primary finger halfway down. This is possibly unusual in the species because two attempts to re-fuse it, once to each of the neighbouring fingers, through a wide phalange, also occur (Wade, 1984). The genus can be traced back from Cenomanian (USSR and USA) to Hauterivian (R.M. Appleby, pers. comm.), and it seems probable that the poorly-known *Grendelius* belongs to this lineage because the basioccipital has no 'peg' overhanging the basisphenoid, like *Platypterygius,* and the much older *Temnodontosaurus platyodon* (Lower Liassic). It also has no very large, ventro-lateral 'apron' of smooth material in posterior view, though not so little as *Platypterygius.* The state of this basioccipital dorsal side is unknown or, at least, unfigured and undescribed. The nature of the pterygoid-squamosal rami is probably unknown because the skull of *Grendelius* was much shattered.

Intraspecific variability includes quite common discrepancies between left and right finblades. Discrepancies arise for example if a digit is rather wide, when a single phalange may be replaced by two, or a single digit by two. The presence or absence of small lateral digits may be taphonomic or natural to the animal (Johnson, 1979). Appleby (1979) recorded one fin pair in which one blade was 4 mm wider than the other, but that is not necessarily as lopsided as it sounds, because the bony blades were surrounded by wide marginal zones of connective tissue, muscle and skin (Andrews, 1924), and could have contained a great deal of internal variation in functionally similar outer coverings. Because of the spontaneous variability about the number of bones in any fin area (McGowan, 1974b, fig. 5; Appleby, 1979, text-figs 1b(i), (ii); Johnson, 1979, many examples), samples as large as possible should be employed in trying to establish a trend. But it is tempting to suggest of *Protoichthyosaurus prososthealis* Appleby (1979, text-figs 2b(i), (ii)), that acceleration has carried the head of a forked mid-fin accessory digit through the distal carpal row into a position where it competed for space with the intermedium. While a wrist-bone could be eliminated by crowding, there was no gap there for a bone to develop spontaneously, without predecessor, in both fins. The addition of partial midfin ulnare digits by longipinnates, which has

been shown in *Eurhinosaurus* and *Platypterygius,* has not resulted in anything like the heteropinnate to latipinnate development. Nor does the addition of posterior and anterior sesamoid digits make latipinnates unrecognizable (*Ophthalmosaurus, Brachypterygius*) since, with the establishment of a second centrale, a median suture was placed below the centre of the latipinnate intermedium, as the two centrales pushed each other into axial positions between radiale and intermedium and intermedium and ulnare. An interdigit suture thus lies below the centre of the intermedium in latipinnates. Now that Appleby has detected the supplementary mid-fin digit in *Protoichthyosaurus,* it should be possible to 'decelerate' and recognize it at earlier stages of development in Upper Triassic material.

More than strict adherence to geometry is required to establish homeomorphy in a morphologic sequence with major time-gaps. Mazin (1983, *vide* Riess, 1985) in establishing a cladistic diagram, and Riess (1986) in simplifying it, have ignored alike the lack of Triassic latipinnates and the presence of earliest Jurassic heteropinnates without a second centrale but with a well-developed digit lying alongside the centrale digit, although often ending a little less proximally. The proximal phalange of this digit having been accepted as a primary distal carpal (once acceleration had carried it into position in the distal carpal row; e.g. McGowan, 1972a, fig. 1c), the latipinnates were classed as having five primary digits. One character by which lateral sesamoid (or auxiliary) phalanges are commonly recognized is that they appear first in axillary positions lateral to two adjoining phalanges of a neighbouring digit (see McGowan, 1972a, fig. 2; 1974a, fig. 1). By this means, and by examining the bones at the proximal end of digits, one or two accessory distal carpals each side of three primary distal carpals have been recognized (Kuhn, 1946, pl. 3, figs 5, 6; Wade, 1984, fig. 2A). Mazin (1983) placed Cretaceous *Platypterygius* with two sesamoid distal carpals anteriorly and two or three posteriorly in an assembly of left-overs with Middle Triassic to Lower Jurassic longipinnates, some without any accessory carpals, the borderline heteropinnate *Leptopterygius,* and *Eurhinosaurus,* each with one accessory distal carpal, and unknown *Grendelius. Stenopterygius,* also with one axillary posterior distal carpal and one corresponding posterior proximal carpal, alongside three aligned proximal and distal carpals in each row, is considered to have four primary distal carpals (McGowan, 1976) and a homeomorph of the captorhinomorph pisiform (Johnson, 1979, illustrates this classic Continental

view adhered to by Mazin, 1983, and Riess, 1986). None of the above workers considers that *Stenopterygius* shared with *Eurhinosaurus* a fin-broadening achieved with retention of longipinnate characters. McGowan (1979) decided that the terms latipinnate and longipinnate were not valid as major taxonomic subdivisions, and they have been used almost to the neglect of other characters. They do seem to reflect valid lineages but too much value has been placed on them.

In the Triassic the niche for rather small, broad-finned ichthyosaurs was filled by *Mixosaurus*; but all Mixosauria died out at the end of the Middle Triassic. In the Rhaetic and earliest Liassic the longipinnates commenced to enter this niche. Fin-broadening accompanied changes which extensively altered the proportions of the whole skeleton (McGowan, 1972a, 1974b; Appleby, 1979), and presumably took the heteropinnate to latipinnate stock into eating habits or habitats in which they did not compete extensively with their forebears, as the broad-fin experiment was repeated in late or mid-Liassic. This time the narrow-finned longipinnates themselves died out at the end of the Liassic.

RESTORATION

Chapman (*in* Taylor, 1987b) has produced a very business-like restoration of an ichthyosaur, non-Martill (1987b). Taylor (1987b), by a careless use of quotation marks, attributed to Wade (1984) use of the terms 'low gear' and 'high gear' for ichthyosaur fin and tail propulsion respectively. Wade used neither, although 'high gear' is very apt, because 'holding station', a term she did use, involves many non-progressive motions like rising to breathe in sleep, or just keeping level in the water when not swimming. Of course, fins may also be used for slow movement where remaining in a certain vicinity is the aim, not progress. For all of these, 'low gear', with its implications of utilizing greater power, and making slow progress, is unsuitable, even though less speed eventuates from fin swimming than tail drive in all normal shapes of fish and, presumably, ichthyosaurs. Massare (1988) points out that fins are energy-efficient at low speeds and tails at higher speeds.

In discussions on locomotion models for ichthyosaurs, most workers seem to have assumed only one style of locomotion per major taxon. Marine animals of normal fish-like adaptations are not so limited (Wade, 1984). They use fin movements for holding station, and sinuous tail movements to progress from place to place, either fast or slowly. Dean (1906) described the rather

restricted movements of a *Neoceratodus fosteri* that had travelled half-way around the world by ship, and was still confined in an aquarium. *N. fosteri*, either free or in a spacious enclosure, make most of their locomotory movements by slow or fast sinuous tail movements like other fish, using their paired fins to hold station, or to brace against the substrate, or to rest there for long periods (A. Kemp, pers. comm., 1988). *Inia*, the Amazon dolphin, lives in waters not famous for pellucid visibility that would make its movements easy to follow. It is usually discussed as seen in its encounters with man. Even in a primitive state, man is a notorious example of sacrificing speed in any one milieu to a wide range of abilities, such as the terrestrial locomotion of an upright observation tower, climbing, and swimming. To associate with man, sociable *Inia* use their idling locomotion, fin propulsion (McGowan, 1974), but that does not mean that they have no means of fast propulsion although McGowan's words 'frequently used for skulling' seem to have been read that way. Riess (1985, 1986) identifies three possible structures of ichthyopterygian tail fin, which he couples to four described forms of locomotion: the *Neoceratodus* type (*vide* Dean, 1906), the *Inia* type (*vide* McGowan, 1972b), the *Leptopterygius* type (Bauer, 1898), and the *Mixosaurus* type (Kuhn-Schnyder, 1964; Appleby, 1979). The first two, from the nature of the models employed, are potentially useful as descriptions of ichthyosaur idling movements, but they are not descriptions of normal progressive locomotion. In view of the decidedly specialized tailfin vertebrae of *Eurhinosaurus* and *Platypterygius*, Riess and Frey's spirited restorations (Riess, 1986) of the *Eurhinosaurus* tail will have to await evaluation by further illustration and documentation of the tail to tailfin vertebrae. The ecologic clash involved in placing *Eurhinosaurus* in a swordfish feeding-type and a '*Neoceratodus*' swimming-type is considerable.

Riess (1985, 1986) redescribed ichthyosaur paired fins, making good use of material recorded by Andrews (1924) and by Owen (1840, 1881). These soft part data he fitted to well-preserved bony finblades, to produce relatively large fins with supple tips and edges. He generalised his description to most types of fin, particularly those with spaces between phalanges, omitting only the *Platypterygius* type of long and wide fins, with a tight bony pavement, already described by Wade (1984) with much the same conclusions, as they were both based on the same soft part literature, and an early study of potential movements by

Oemichen (1938). As Riess' thesis must have been well-advanced when Wade published, similar ideas must have occurred to both. Riess favours a very upright position for the scapula and clavicle, like Johnson (1979). The distal end of the Stewart Park *Platypterygius longmani* specimen, with clavicle and scapula associated with ribs and vertebral column, has the clavicle and scapula almost parallel to those vertebrae still in natural position, but the ribs are distorted, straightened by flattening (Wade, 1984, fig. 2c). The left scapula and clavicle of QMF2453 were found in a closely similar position but became detached during acid preparation. They are not conclusive evidence against Riess' interpretation, for the coracoids of one were displaced and those of the other were lost. In *Platypterygius* the scapula is widened enough distally that even in Riess' reconstruction, it could have rested on two ribs. This might have sufficed for an aquatic animal, though not for the girdle of a weight-bearing limb. Preservation is not adequate to indicate the shape of the probable cartilage termination of the scapula.

Taylor (1987a) has offered a new interpretation of the direction of thrust generated by ichthyosaur tails, demonstrating that thrust could have operated at the 'centre of balance' (*sic*) rather than at the downward angle at the centre of gravity previously used in calculations (e.g. see McGowan, 1973b). Taylor's stress on neutral depth as the hunting or cruising depth is perhaps a little precise for nature; hunting depth is generally the depth that best suits the prey of the season, not necessarily the hunter. The ability to adjust 'neutral depth' quickly would be the best adaptation for a hunter to acquire. Restorations sometimes show

ichthyosaurs letting out air under water, but they are unlikely to have opened their nostrils while in action under water. Broadly attached fins, such as *Platypterygius* seems to have had, are rather stiffly attached to the body, as in sharks of comparable size, but sufficiently flexible outwardly (Wade, 1984; Taylor, 1987a) to allow any direction of steering. Wade's suggestion of a slight upward set on the main part of the fins of *Platypterygius*, even when diving, was stress on a safety factor. Airplane wings similarly tilt up to the front for stability. Most of the potential problems that would have arisen from allowing the huge front fins to be pressured from above would have been due to forward movement. The effects of negative pitch (hopefully not present for Taylor, 1987a) and slightly *greater* (not lesser) density than water would have been comparatively minor. Taylor's attempt to summarize McGowan's work and Wade's (which were not in full agreement) in the same sentences rendered him incomprehensible at that point, but he presented his own thoughts more successfully. He described a pitching action which was presumably used, though commonly not as vigorously as figured (Taylor, 1987a, text-fig. 2) in normal breathing. The most economical way to breathe was to break water with as little of the head as possible. Cruising cetaceans normally reach the surface in an asymptotic curve that just breaks the surface as the animal finishes breathing out. Using an adjustable plasticene model, it is possible to see that if the *Platypterygius* snout was straight, most of it would emerge at the top of an asymptotic curve swum high enough to bring the nostrils above water. But long ichthyosaur snouts, as seen in *Platypterygius longmani, P. americanus,*
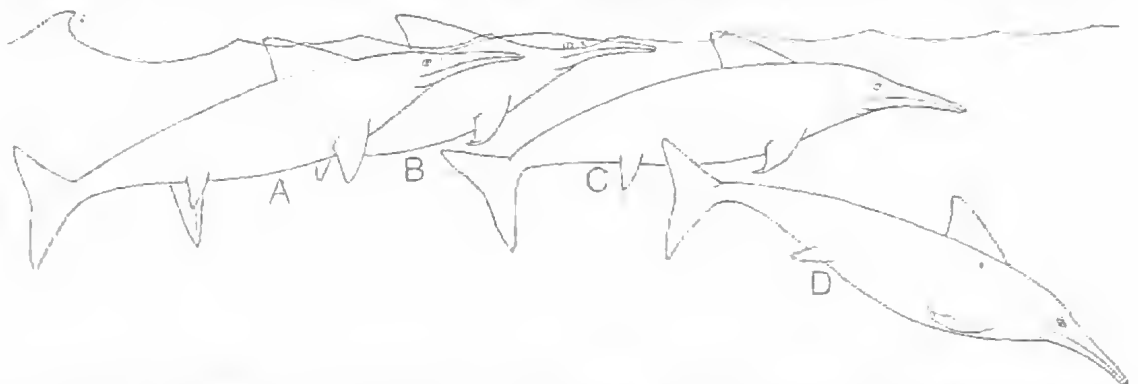

FIG. 7. Sequence of diagrams to demonstrate *Platypterygius longmani* surfacing to breathe at cruising speed. Diagrams C and D may be interpreted as alternatives or as a sequence. Fineness ratio (length from front of orbit/maximum depth of body) varies between 4.6 and 4.8 because of the animal's ability to modify flexure of the tail. As restored the tailfin comprises 80 cm of vertebrae plus terminal cartilage. Approximate ratios of head : body + neck : whole tail are 3:5:4.

Temnodontosaurus tenuirostris and *Lepto-pterygius acutirostris*, and even some medium and short snouts e.g. (*Ichthyosaurus breviceps*), dip down toward the tip. Their snouts probably broke water only with part of the upper surface (Fig. 7). The pineal organ presumably informed the animal about waves or other surface conditions of the water-cover, by pressure or light intensity, or both, prior to air exposure.

The top of the head would have had to be exposed in breathing, but whether much of the dorsal side of the neck or shoulders were usually exposed would have depended on the relative effort required to bend the neck or lift that part of the body above the water. It is quite likely to have been individually variable. Since fins are designed for use in water, it is certain that lateral fins were not flourished in the air save in desperation or display. The head is a long or short inflexible front segment to the axis, but maximum possible movement on the occipital joint of *Platypterygius* was probably 10° in a vertical plane (direct measurement from VMP12989) and the same laterally. Half of that suppleness would have sufficed for diving during breathing, to judge by films of cruising whales. The antero-dorsal neural spines each overlapped the succeeding centrum, but the postero-dorsal and following caudal vertebrae were confined only by the zygapophyses and the massive longitudinal muscles attached to neural spines situated above their own centra; 1° freedom per average vertebral joint would have supplied more than enough suppleness laterally, and the total of 30° or more bend in the dorso-ventral plane was adequate for diving, if the variable tail bend was not enough. Massare (1988) evaluated the likelihood of suboscillatory or oscillatory caudal fin action for progressive movement and preferred oscillatory, as the proportions of the tail resemble dolphins, which use oscillatory action. The tail-base vertebrae of *Platypterygius* were commonly largest, but some specimens had a very gradual slow increase in size and were almost stable from early postero-dorsal into the tail, before diminishing. Thus the tail base was one of the least flexible parts of the axial column, and this would not only have made it relatively strong, but would have tended to minimize the yaw incipient in tail-swing. If Martill (1987b) was correct that there was no dolphin-like or shark-like dorsal fin to stabilize the body against yaw and roll, then an alternative structure was needed, and an alternative explanation for the V-shaped articulation surfaces on *Platypterygius* neural spines 11 to 20+. Although cartilage extensions dorsally could

support varied shapes of mid-dorsal ridges, all are effectively dorsal fins. Martill pointed out that a great difference between dolphin shape and ichthyosaur shape was the retention of the rear fins throughout ichthyosaur history. These he suggested controlled 'roll'. Rather than working in tandem with the fore fins, the rear fins, situated immmediately below and to the sides of the largest diameter of the axial column, may well have had the task of helping to compensate for yaw by exerting a counter-drag on the centre of gravity. This new-old idea has also been mentioned recently by Taylor, who did not comment that hindfin compensation for yaw would be applied virtually in the same plane as the tail thrust if the old model for thrust were correct. It is time someone competent in marine architecture had a say!

Wade (1984, pp. 108-11) discussed the functioning of *Platypterygius* in general terms, concluding like Taylor that the tail provided the main driving force and the pectoral fins did most of the steering. Massare (1988) came to the same conclusion in her much more significant study. After comparing potential ichthyosaur densities with what is known of crocodiles and sea-snakes, Wade (1984, pp. 108-11) concluded: 'Whatever the density of extreme juveniles, older ichthyosaurs were probably as dense as sea-water' [at the same depth is implied] 'or a little denser. Comparison favours slight negative density'. The propensity to float, crocodile-like, at the surface she also attributed to ichthyosaurs. The mechanism by which a floating crocodile changes to a sinking crocodile has now been described as exhaling slightly before closing the naris (Green, 1988, p. 20) and Molnar (pers. comm.) tells me it is easily observed in small specimens (these would have to exhale relatively more air). It is a mistake to simplify the activities we attribute to animals known as fossils from the not-far-distant past to something much more elemental than is seen today.

THE LAST ICHTHYOSAURS

Platypterygius longmani lived through to the end of the Albian, at least, but *P. americanus* and *P. kiprijanoffi* lasted well into the Cenomanian. Nesov *et al.* (1988) have listed the ichthyosaur fauna of USSR as background to the apparent extinction of ichthyosaurs linked with the 'great turnover of ecosystems in the period from Cenomanian to late Turonian'. Taylor (1987b) did not give a reason for his recent assertion that ichthyosaurs lived to the end of the Cretaceous, which is unlikely. Baird (1984) has removed a number of scattered bones from contention, and

the putative 'last' record is by Teichert and Matheson (1944) from the Lower Santonian of Dandaragan, Western Australia. Their collection consisted of eight ichthyosaur (and eight plesiosaur) centra and other bones. They were recovered by the seiving of an exploratory sample for a commercial phosphate open-cut mine, so their original disposition is unknown. The deposit was a fossiliferous nodule bed. Fresh breakage aside, the ichthyosaur postero-dorsal centrum figured is relatively undamaged; natural features such as the ventro-lateral rib apophyses, neural arch facets and margins of the centrum are figured as unworn. The three views given do not suggest derivation from older rocks, though that is possible. This and the other ichthyosaur bones are within the range of variation of *Platypterygius* and a number of other ichthyosaurs, and Teichert (*in* Teichert & Matheson, 1944) correctly did not identify them. Teichert suggested that the species here named *Platypterygius longmani* might be a *Myopterygius*, (*Platypterygius americanus* (Nace) was known as *Myopterygius americanus* at the time), and this name is found in collections and semipopular literature from time to time.

ACKNOWLEDGEMENTS

From the first my studies were aided by a generous supply of reprints from Dr C. McGowan of Royal Ontario Museum, and later by discussion and correspondence with Dr R.M. Appleby, University of Hull, and by his permission to cite the correspondence. Dr R. Wild of Paläontologische Abteilung des Staatlichen Museums für Naturkunde in Stuttgart very kindly demonstrated the beautiful Holzmaden ichthyosaurs in his care, and Professor Kuhn-Schnyder facilitated my viewing the Tessin mixosaurs at the Paläontologisches Institute und Museum der Universität, Zurich. The British Museum ichthyosaur display was also viewed, and C. Walker showed me some of the material in storage. Dr T.H. Rich of the Museum of Victoria facilitated the loan of material studied by McCoy (1869), and gave permission to prepare it, while Dr T. Darragh produced Sutherland's letters of conveyance for scrutiny. Dr R. Molnar of Queensland Museum has provided a helpful sounding-board for ideas and further access to literature. Readers will benefit from the editorial review Dr R.A. Thulborn provided.

I am grateful to all these helpful people, and also to those who have donated original material, from James Sutherland and J. Edgar Young to Charles and Andrew Robinson and Mrs Hazel Young.

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